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Marine Microcosms in Ecological Research

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ABSTRACT

The use of microcosms in marine research is a recent development, beginning in earnest in the early 1960s. The level of effort during this time has ranged from that of single investigators with small flasks to complex multi-institutional programs using 1300-m^3 containers. A major recent trend is the use of microcosms as living models of specific natural ecosystems or types of systems, in contrast to earlier research that tended to use microcosms as small-scale environments in their own right in which certain properties and processes common to all ecosystems might be studied. Microcosms have always been used in research dealing with species succession, predator—prey interactions, etc., and much recent work has emphasized their use to explore the biogeochemical cycling of various materials, especially pollutants, and the effects of these materials on the biology and chemistry of marine ecosystems. This approach has generated interest in the problems involved with microcosm design and operation and the interpretation of complex multiparameter data sets obtained from supposedly replicate microcosms over long periods of time. Attempts have been made to design experimental systems in which light, flushing, surface-to-volume ratios, and turbulence are scaled appropriately and to evaluate the consequences, if any, of the exclusion of larger animals. The influence of size on microcosm behavior is yet to be fully assessed. There appears to be little in the way of ecological theory that is very instructive in addressing any of these questions, and most workers either avoided a rigorous attempt to scale their systems or resorted to a time-consuming iterative empirical approach. The interpretation of scaling experiments, as well as other microcosm studies, is made more difficult by lack of any general operational definition of success in microcosm behavior. It is not clear how closely and with respect to which parameters a microcosm must follow the natural system to be considered an acceptable model. There is not even agreement that it is in principle possible for a microcosm to track the natural system very well. Also, it is not clear how the variance that seems to be inherent in the behavior of replicate microcosms

should be viewed. Since nature is extremely variable, it can be argued that replicate microcosms cannot model nature well unless they also display considerable variation. For this reason, it may be necessary to observe replicate microcosms over relatively long time periods to obtain a reliable overall record of system behavior. Despite the many difficulties, results from a number of marine microcosm studies suggest that rigorous attempts to design and operate microcosms as models of particular systems can yield useful and exciting information about both biological and chemical features of natural systems.

In setting out to discuss how microcosms are made and their uses, our first task was to think of a title for the paper. One that came to mind was "The Application of Japanese Bonsai to Coastal Marine Ecosystems." By a process of association, this led to a general observation about the nature of human beings. Throughout recorded history a sizable fraction of the people who were able to do so have, in various ways, attempted to keep captive and maintain in miniature a portion of nature. Many people appear intensely fascinated with such activities. These drives are manifested in the keeping of a remarkable range of ordinary and exotic animals as pets or in zoos, the keeping of aquariums of various types, and the keeping of houseplants and botanic gardens. This apparently innate characteristic of human beings must have been important initially in the development of animal husbandry and agriculture. These activities are now usually considered recreational, but a great deal has been learned about nature by observing the behavior of, for example, organisms in aquariums. The fascination with keeping bits of the world captive in bottles and recent developments in understanding the complex interactions in natural systems—the science of ecology—have led to attempts to keep portions of whole ecosystems enclosed for study.

As we understand the use of the word microcosm today, it normally excludes the usual aquariums and single-species cultures. Microcosms are portions of ecosystems or living models of ecosystems enclosed and maintained for observation and study. Although there are important exceptions, the usual intention of microcosm builders appears to be that the microcosm should in principle be self-maintaining over time, without the need for outside supplements of organic matter or nutrients. Microcosms encompass a broad range of structural types and approaches to observation and experimentation. They include gnotobiotic microcosms, in which several species are placed together so that their interactions can be observed [e.g., those described by Nixon (1969), Taub (1969), and Taub and Crow, this volume], and microcosms made by isolating a portion of nature with most or all of its species included. In

comparison with the number of efforts to develop microcosms of terrestrial, stream, pond, and lake organisms and ecosystems, relatively few attempts have been made to examine marine ecosystems by enclosure in microcosms, and the goals and rationale have varied widely.

Representative marine microcosms and approaches are listed in Table 1. Some of these facilities were run primarily as culture vessels or aquariums to observe plankton blooms or other relatively short-term physiological or behavioral features of the inhabitants rather than as microcosms, but the distinction is often somewhat arbitrary. The list includes a spectrum of sizes, ranging from 19-liter glass carboys to 1300-m^3 bags of the Controlled Ecosystem Pollution Experiment (CEPEX), and of effort, ranging from one-person operations to complex interdisciplinary programs involving 40 or more people. The table contains only two references to microcosm use before 1960. Microcosms have been used for various purposes for a long time, but attempts to maintain marine ecosystems in this way appear to be recent.

Microcosms have been established for three major reasons:

1. To gain an understanding of biological interactions in complex systems and provide data for testing various hypotheses in ecosystem theory
2. To study the effects on the systems of such perturbations as the introduction of sewage, oil, or trace metals and changes in temperature
3. To study the biogeochemical behavior of various substances of interest, usually pollutants

Most attention has focused on item 1 and least on item 3. This is because we do not know very much about the complex mechanisms that operate in any ecosystem, and there has been a suspicion that it would be unwise to extrapolate from microcosm observations to the expected field behavior of most substances. In addition, the interest of most biologists involved in this research has been directed toward understanding how complex assemblages of organisms pass through successional stages and eventually live together in a more or less steady-state situation (Beyers, 1963; Cooke, 1971; Odum, 1969). To this end many of the early marine microcosm studies were focused on general descriptive features of ecosystems, e.g., diel patterns of dissolved oxygen and pH, biomass, ratio of total system production to respiration, and species diversity.

Recently, however, there has been an increasing interest in using marine microcosms to carry out specific perturbation experiments with various pollutants and to explore the biogeochemical cycling of

TABLE 1

REPRESENTATIVE MARINE MICROCOSMS

Type and location	Characteristics	Reference
Glass carboys, Texas	12 19-liter carboys, with sediment	Abbott, 1966
Plankton, British Columbia	Spherical bag, 100 m^3	Antia et al., 1963
Benthic community, Rhode Island	Tanks, 4 m^2 by 0.5 m deep, running seawater	Blake and Jeffries, 1971
Tall plankton tower, Halifax, Nova Scotia	One tank, 100 m^3 (10 m^2 by 10 m deep)	Conover and Paranjape, 1977
Salinity gradient, Texas	Six sets of five 31-liter coupled containers	Cooper and Copeland, 1973
Plankton, Loch Ewe	Moored plastic bags, 100 m^3	Davies, Gambel, and Steele, 1975
Bay plankton, Chesapeake Bay	Plexiglass cubes in situ, 1 m^3	Heinle et al., 1979
Tropical reef, Hawaii	24 tanks, 1.37 m^2 by 0.46 m deep	Henderson, Smith, and Evans, 1976
Salt marsh, South Carolina	Tanks, 6 m^2 by 1 m deep, tidal flushing	Kitchens, 1979
Saltwater ponds, North Carolina	Six ponds, 500 m^2 by 0.5 m deep	Kuenzler, Chesnut, and Weiss, 1973
Plankton, The Netherlands	Four floating bags, 1.4 m^3	Kuiper, 1977
Plankton, France	About 30 bags, 0.5 m^3	Lacaze, 1974, 1976
Plankton (CEPEX), Sannich Inlet, British Columbia	Moored plastic bags, 1300 m^3 and 70 m^3	Menzel and Case, 1977
Tall plankton tower, California	One tank, 70 m^3 (7 m^2 by 10 m deep)	Mullin and Evans, 1974
Various ponds, Texas	Grass, reef, and algae in concrete ponds	Odum et al., 1963
Bay, plankton and benthos, Rhode Island	12 150-liter plastic tanks, with sediment and benthos	Oviatt, Perez, and Nixon, 1977
Tall plankton tower, Göteborg, Sweden	One tank, 37 m^3 (3 m^2 by 12 m deep)	Petterssen, Gross, and Koczy, 1939
Bay, plankton and benthos (MERL), Rhode Island	12 tanks, 2.6 m^2 by 5 m deep, sediment and benthos	Pilson et al., 1977, 1979; Pilson, Oviatt, and Nixon, this volume
Concrete salt ponds, Massachusetts	Four tanks, 3.9 m^2, fertilized	Pratt, 1950
Plankton tower, Baltic Sea	4 plastic cylinders, 3 m^2 by 5 m deep, attached to sediment	Von Bodungen et al., 1976
Tidal mud flat, The Netherlands	25 m^2 by 1 m deep, tidal exchange	Wilde and Kuipers, 1977

materials. The shift toward using microcosms as experimental tools has placed an increasing emphasis on the credibility of the microcosm as a reliable analog of large-scale nature. The early users of flasks and carboy microcosms were looking for general patterns of, for example, autotrophic succession in reasonably complex systems. The validity or usefulness of their results did not necessarily require that their flask communities resemble any particular piece of nature very closely. However, as we have begun to use microcosms to study the responses of particular marine ecosystems to specific perturbations and the behavior of pollutants within the systems, the issue of correspondence between the living model and nature has emerged as a major question for those doing microcosm research and for those who hope to use the results from microcosms to develop management policies.

This issue of correspondence is a very difficult problem that also appears when evaluating numerical ecosystem models (Kremer and Nixon, 1978). In the case of both living and numerical models, there are no generally agreed upon qualitative or quantitative criteria for success. At this time it is not possible to give a general objective description of a successful microcosm. We do not know which parameters are most important to have in agreement or how similar they must be to be considered in agreement. To some degree this reflects the diversity of goals and approaches being pursued with microcosms, but to a large extent it reflects our lack of knowledge and understanding of ecological systems in general and in particular. At present much of microcosm design is still iterative and intuitive—we are designing tools for a task we do not yet fully understand. Much was learned from the early exercises of dumping mud and water into containers to see what would emerge, but the increasing emphasis on designing and operating microcosms to develop and maintain specific kinds of ecosystems is forcing us to grapple with basic questions about the organization and dynamics of nature on all scales. Microcosms are nature made smaller but not necessarily simpler.

DIFFICULTIES AND CHALLENGES

In designing any microcosm it is important to consider whether the behavior of the system will be seriously affected by scaling various physical parameters or by excluding higher trophic levels. An additional consideration is that there should be statistical validity to the results, but how this should be addressed is not as simple as it might appear. In general, the ecological literature provides little

experimental evidence to guide us. As examples of known or possible difficulties, let us consider the following.

Size

Marine microcosms spanning a broad size range have been set up, with a factor of 70,000 between the smallest and largest (Table 1). If we include the flasks of Margalef (1967), the factor is more than 10^6. With such an enormous range in size, there must be some difference in behavior or in the "validity" of the behavior of the enclosed ecosystem as a function of scale. The common feeling in setting out to build microcosms, at least those thought to enclose pieces of real nature, appears to be that "bigger is better." Accordingly, large amounts of money and effort have been spent to build a number of the larger microcosms, without clearly establishing that the size was needed for the purpose of the study. For example, an experiment with systems containing four trophic levels might be accommodated in 1 or 2 cubic centimeters of sediment, with microbes through meiofauna, or in several hundred cubic kilometers of oceanic water, with diatoms through anchovies to squid and pilot whales. For studies of the theory of interactions in multispecies communities, the small microcosms would seem to be more efficient.

There have been few attempts to study the effect of size on microcosm behavior; two recent studies in fresh water are those of Maguire et al. (this volume) and Harte et al. (this volume). One of the few attempts to study the effect of scale in marine systems is that of Adler, Amdurer, and Santschi (this volume), who compared the behavior of several trace metals in the 13-m^3 Marine Ecosystems Research Laboratory (MERL) microcosms with that in the 150-liter microcosms set up indoors under artificial light at the Environmental Protection Agency (EPA) Laboratory in Narragansett. The smaller EPA microcosms have about 1% the volume of the MERL tanks, but the behavior of the metals was similar in both. This result suggests that experimental efficiency can sometimes be improved by carrying out more experiments more cheaply in small microcosms and that the biogeochemical behavior of substances may be less sensitive than biological activities to variations in conditions.

Lower size limits may be set by the practical consideration that repeated sampling should not deplete the stock too much, and upper limits may be set by the cost of achieving statistically adequate replication. It is plausible that increasing size in most systems will lead to increased heterogeneity of the system. We are unable to speculate on whether increased heterogeneity would lead to greater or less randomness in behavior, but it would probably lead to greater stability, when viewed over the appropriate time course.

Sediment–Water Ratio

About half the microcosms considered here explicitly include sediments (Table 1). Sediments are known to play an important role in recycling nutrients in coastal areas. Nevertheless there have been few studies of microcosm behavior according to the ratio of water volume to sediment surface. The microcosms described by Perez et al. (1977) and Oviatt, Perez, and Nixon (1977) had a small box of sediment hung inside a 150-liter microcosm so that the ratio of water volume to sediment surface area was equal to that in Narragansett Bay. The sensitivity of microcosms to this parameter was explored in one experiment but was not fully established. This adjustment must be applicable only over a limited range. In a thought experiment we can imagine an extreme case where the natural system simulated is, for example, 1 mile deep (1500 m) and the ratio of volume to surface area would, therefore, be simulated by 1 cm^2 of sediment in a 150-liter microcosm. In this case the sediment would probably be grossly abnormal. Evidently systems in which distance and time are important in the exchange processes will be very difficult to simulate. It is no easy matter to see how to modify a successful shallow-water microcosm to simulate even a continental-shelf situation, if this parameter is important.

Light

Microcosms have been set up outdoors and indoors. When the microcosm simulating some natural system is indoors, a common approach is to attempt to provide artificial light that approximates that of the sun in spectral composition or to match the intensity and spectral composition of light at some distance below the surface in nature. If the outdoor microcosm is that of a salt marsh (Kitchens, 1979) or a tropical coral reef (Henderson, Smith, and Evans, 1976; Henderson and Smith, this volume), then natural sunlight is appropriate. If a planktonic community is to be simulated, however, certain problems arise. If attempts are made to examine the necessary scaling to account for the generally shallow depth of the microcosms, the ability of phytoplankton to adjust their physiological responses to various light intensities, and the timing of these adjustments, the problem becomes infernally complex. Kremer and Nixon (1978) and Nixon et al. (1979) discussed these difficulties. Nixon and coworkers, using the 150-liter microcosms (Perez et al., 1977), attempted to simulate the onset of the winter–spring bloom in Narragansett Bay, which generally occurs in the bay when the incident light reaches an intensity of about 200 langleys/day and the average light intensity in the water column is about 40 langleys/day.

At these light levels, however, the microcosms rapidly developed massive blooms. After some experimentation they found that the onset of the bloom would occur in the microcosms when the average light in the water column was only about 3 langleys/day and that this level would provide a reasonable match to the growth rates observed in the field. The effects of shallow depth, differences in the apparent extinction coefficients in the microcosms compared with those in the field, and adjustments by the plankton to low light intensities combined to produce very difficult problems in scaling.

Any attempt to simulate nature in small microcosms where light is important may require empirical experimentation. The use of large microcosms deep enough to approach natural water columns may alleviate these problems but will not eliminate them.

Turbulence

Turbulent energy appears to play a significant role in the behavior of planktonic ecosystems (Perez et al., 1977; Nixon et al., 1979; Harte et al., this volume). The rate at which turbulent energy is expended in any system and the scales of the motions involved are extremely difficult to measure, however, and at the present time come close to defeating both the theoretician and the experimentalist in fluid dynamics. Several attempts to measure the regime of turbulence in the MERL tanks and to compare this with the reference natural system are presented by Nixon et al. (this volume). Although several techniques produced results that converged toward similar quantitative estimates and understanding of the processes involved, some results were contrary to our understanding. It seems we still have a long way to go.

We believe that difficulties in understanding and measuring turbulence have held back the development of our understanding of planktonic processes and our ability to keep plankton-based systems in microcosms. The development of a handy "turbulence meter" would be followed by a burst of activity and increased knowledge in this area.

Exchange of Water

Some microcosms have been run as quite open systems fed by a strong flow of water (Blake and Jeffries, 1971; Henderson, S[illegible]h, and Evans, 1976). These are not complete microcosms in that they are partially isolated portions of a much larger system from which they derive nutrients at least (reef microcosms) or all of their biochemical energy from inputs of carbon fixed elsewhere (benthic microcosms). They are living models of such dependent parts of the larger system.

Most microcosms have been operated as batch cultures, but allowing some exchange with their surroundings or treating them as a form of chemostat has many advantages. Margalef (1967) discussed the use of chemostat-type microcosms, and Cooper and Copeland (1973) set up flowing microcosms with an estuarine salinity gradient. In fact several of the microcosms listed in Table 1 were operated as open systems to some extent. Nevertheless there have been few attempts to experiment on the exchange rate to see how this affects the behavior of the systems. Cooper and Copeland found that changing the ratio of fresh to salt water input changed the behavior of the systems considerably, but that involves more than the effect of exchange per se. Perez et al. (1977) compared the behavior of the 150-liter microcosms operated with water-turnover times ranging from 7 to 100 days. The effect on the systems was almost nonexistent. There were increased numbers of grazers at the longer turnover times, but the standing stocks of algae and nutrients were unchanged. In the MERL tanks during a 7-month period of comparison, it was difficult to find substantive differences in behavior between tanks operated in a batch mode and those operated with a turnover time of 27 days (Pilson, Oviatt, and Nixon, this volume). This result surprised us because we had thought it intuitively obvious that there would be major differences under the two regimes.

Predator Exclusion

A commonly held view is that community structure generally is powerfully influenced by the activities of top predators. This effect is strikingly demonstrated in rocky intertidal communities (Connell, 1972), and there are many other places where it must be important, e.g., kelp beds (Mann, 1977) and the reef microcosms of Henderson, Smith, and Evans (1976). If all communities are so controlled, it follows that no marine planktonic community can be maintained in a microcosm for long periods of time because the natural foraging area of a white shark or a killer whale is too large for enclosure to be economically feasible.

It has not been demonstrated that all the various trophic levels of planktonic communities are always tightly coupled, however. There is some evidence to the contrary, and also evidence suggests that the intensity of the interaction is seasonally variable (Hitchcock and Smayda, 1977; Kremer and Nixon, 1978; Oviatt et al., 1979). For considerable periods of time, both the 150-liter microcosms of Perez et al. (1977) and the MERL microcosms (Pilson et al., 1979) maintained phytoplankton communities that were, as far as could be

ascertained, quite similar to those in Narragansett Bay, both in total biomass and in species composition when the zooplankton biomass was quite different from that of the bay. Neither set of microcosms had large fish, but blooms of carnivorous ctenophores did occur in the MERL tanks and the sampling of zooplankton in the MERL tanks imposed a predation effect of about 15% per week. These effects seem unlikely to have mimicked nature very closely, yet for a considerable time the phytoplankton did. If this apparent lack of tight coupling between various components of the plankton continues to be borne out by further observation (and no doubt the situation will vary greatly according to circumstances), it will be an asset to the development of microcosms containing a planktonic component.

Surprisingly, experiments on the effect of predation on the structure of soft-bottom communities in Narragansett Bay have also failed to demonstrate a marked effect. Nixon et al. (in preparation) kept sediments and benthos in large tanks (6 m in diameter) with flowing seawater and exposed segments to predation by 10, 3, and 0 flounder. Even though the fish in the 10-flounder segment were not getting enough to eat (as evidenced by weight loss), the macrofauna and meiofauna in the sediment were not detectably different in numbers and biomass from those in the 0-flounder segment. Rates of nutrient flux from the bottom also were not different among segments. These puzzling observations suggest that the influence of bottom-feeding fish on soft-bottom communities in this area may be less than had been imagined. These results were also duplicated by data from exclusion cages placed in the field. Evidently the question of predation effects is complex, and the world is full of surprises. These results suggest that exclusion of the larger foraging fish may not have a strong direct adverse effect on the infauna of soft-bottom communities and that these communities may, therefore, be relatively easy to keep in microcosms.

Variable Behavior of Nature and Microcosms

Ecologists have learned to live with the variability and patchiness of nature. In making microcosms, however, most people feel that replicability is important. After all, it is difficult to carry out an experiment if the replicates do not replicate very well and there is more variance within than between treatments.

In dealing with constructed microcosms containing few species and operated to constrain their behavior as much as possible, it may usually be desirable to achieve maximum replicability, even to the details of individual species activities. Most marine microcosms are

made by isolating a piece of nature, however, and there has been concern that they act in a way not widely divergent from the natural system to which they are analogous. If they are to be used to study fates and effects of substances, then, although we admit that no microcosm can ever be an exact replica of nature, we still want them to be "not too abnormal." Their differences from the natural system should be reasonably well defined so that the effects of the differences can be evaluated.

The existence of variability is a severe problem, becoming even philosophically difficult to deal with. Nature herself does not replicate well. Every patch of water follows its own course to some extent, exchanging all the while with its surroundings. Every bay and cove is to some measurable extent unique. In Narragansett Bay the timing of initiation and duration of blooms and species composition and succession in the blooms vary from place to place and from year to year throughout the bay. Although several of the physical forcing functions exert considerable control on the timing and magnitude of events in the bay (Smayda, 1957; Hitchcock and Smayda, 1977; Kremer and Nixon, 1978), there is a considerable apparent randomness as well. Probably this is inherent in the system and is compounded, as it must be, of hundreds of causes. An exact prediction of the total behavior of such an ecosystem will always be impossible.

Given this situation, we face a dilemma. First, if a set of microcosms replicate their behavior closely, the probable causes are that they do not contain or encompass many of the elements responsible for the apparently stochastic or random behavior of the natural system or that their behavior is strongly driven by whatever forcing functions are applied, more so than are most natural systems. In either case they will not behave very much like the natural system to which they are supposed to be analogous. Depending on the purpose for which the microcosm is run, this may be acceptable or even desirable. We should understand what is happening, however.

On the other hand, if the intention is to operate microcosms that are similar to nature, so that most of the major activities are carried out at similar rates and by mostly the same species as in the natural reference ecosystem, it follows that we should let the systems live as they do outside. Then the stochastic behavior of nature will intrude. Just as each bay or patch of water goes its own course, so will each microcosm, and they will not replicate well.

The foregoing argument leads to the conclusion that the better the microcosm the worse it replicates and, therefore, the worse it is as an experimental tool. There must be some way out of this morass. We must develop a perspective to see the systems function over the

appropriate time course and a realistic sense of their stochastic behavior.

Let us consider examples from early and recent microcosms. Abbott (1966) examined the replicability of 12 identical microcosms maintained in 19-liter glass carboys. By most standards of laboratory experimentation, the replicability was dreadful. When measured at the end of 30 days, the nutrient concentrations showed coefficients of variation ranging from 22% for nitrate to 73% for phosphate. Variation of respiration was 32% and that of primary production 14%. If we cannot do better than this, what hope is there? How can we use microcosms with this kind of variability in chemical composition to experiment on routes, rates, and effects of other chemicals that we know far less about?

Data from the MERL microcosms were taken weekly throughout a year (Pilson, Oviatt, and Nixon, this volume), and phosphate concentrations in three control tanks are plotted in Fig. 1. Obviously the coefficients of variation must vary from 0 to 50 or 100%, depending on when the observations were made. If we had only a single set of samples, the data would be quite discouraging. The discouragement is in part an artifact of when the sampling is done and of slight variations in the timing of various events. The plot of the year's data (Fig. 1) would convince anyone that the three tanks tracked each other remarkably well, showing essentially similar behavior, with some random noise and slight differences in the timing of major events. The tanks also tracked the waters of Narragansett Bay (Pilson, Oviatt, and Nixon, this volume).

Evidently free-running, complex systems that are allowed to behave as naturally as they can will show some stochastic elements in their behavior, and observations must be maintained over a long time period to see both the real similarities and the real differences in behavior. Long-term observations are also important if we are studying the effects of perturbations on the systems since biological effects and the biogeochemical behavior of introduced substances will no doubt vary seasonally, at least outside of tropical regions. This latter point was also emphasized by Oviatt et al. (1979) and Bowling et al. (this volume).

Chlorophyll-a concentrations in the same three MERL control tanks measured weekly for a year did not track each other nearly as well as did the phosphate concentrations (Fig. 2). Usually the chlorophyll concentrations differed considerably from tank to tank, but the data for a full year show that certain remarkable similarities existed as well. All tanks exhibited a dramatic algal bloom in the late fall and a decrease in phytoplankton density after the bloom. All tanks showed a series of increases and decreases in phytoplankton

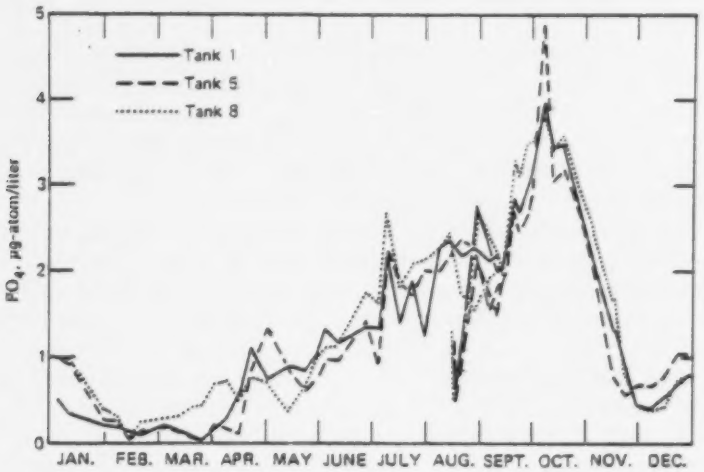

Fig. 1 Concentrations of dissolved reactive phosphate in MERL tanks 1, 5, and 8 (control tanks) measured weekly between Aug. 16, 1976, and Sept. 12, 1977. (From Pilson, Oviatt, and Nixon, this volume.)

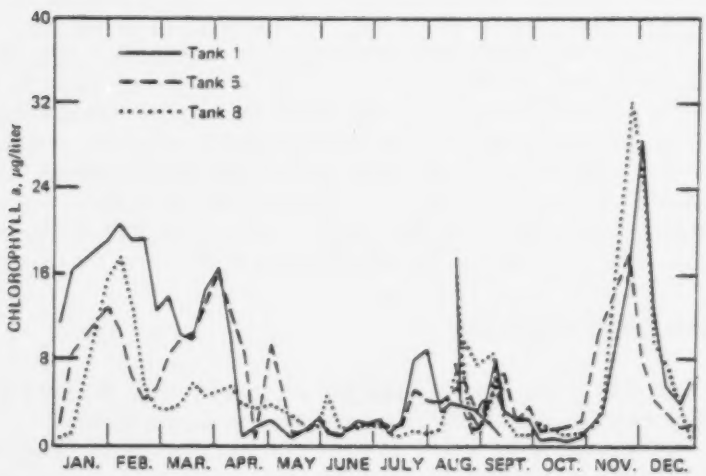

Fig. 2 Chlorophyll-a concentrations in MERL tanks 1, 5, and 8 (control tanks) measured weekly between Aug. 16, 1976, and Sept. 12, 1977.

concentration in the early spring, but the exact timing of each was not coincident. All tanks showed low chlorophyll concentrations in the early summer and a series of blooms during the middle and late summer.

Such evidence as we have (e.g., Smayda, 1957, 1976; Kremer and Nixon, 1978) shows that the bay also exhibits apparently random blooms and decreases in phytoplankton concentrations. We do not know, however, whether this behavior of the bay is more or less variable than that of the three tanks. Spatial considerations are difficult to account for in assessing this question.

Variable behavior of the natural ecosystem provides an envelope of uncertainty about our understanding of natural systems and our quantitative knowledge of their average behavior. This envelope is quite large and sets a severe limit on the sensitivity with which we can reasonably hope to measure the impact of a change in the physical forcing functions or of some chronic pollutant on the natural system. This same uncertainty also exists for microcosm work, and in some sense it can be reduced only by losing some essential elements in the behavior of the systems. We believe this problem may be inherent and inescapable.

We do not believe, however, that this difficulty necessarily weakens the microcosm approach to ecosystem investigations. In the first place, the behavior of chemical substances in microcosms seems to be more conservative than that of biological organisms (further experimentation should be directed toward examining this question) so that data on chemical behavior may be less subject to such random vagaries, especially if fairly long-term series are taken.

Second, the stochastic behavior of biological elements in the microcosm can be taken as a positive feature, especially if some attempt is made to compare this with the natural reference system and to make sure that the species composition is not permanently abnormal. There is no substitute for plotting and examining data in long time series, but multivariate techniques may also be useful for comparing complex data sets (Pilson et al., 1979; Oviatt, Perez, and Nixon, 1977; Oviatt, Walker, and Pilson, 1979).

SUMMARY OF PROBLEMS

At this point let us summarize some of the difficulties and problems with marine coastal microcosms as we see them.

1. We need more work on the effect of size per se. This would have economic value in improving the information returned per dollar expended.

2. Questions of the scaling of various physical parameters—light, turbulence, water–sediment ratios, exchange of water, and no doubt others—and the interactions of these parameters need to be more explicitly addressed.

3. The question of predation will persist and needs to be continually evaluated in each system.

4. The stochastic nature of nature and of microcosms run to simulate nature must be considered in a way appropriate to the problem. We may want to think of variation on a certain scale as a good feature, and we ought to compare it with the variability of nature. We must find realistic ways to compare the stochastic behavior of nature with that of microcosms. We must find statistical approaches which do not hide much of the real information present in the long time series of complex data sets that microcosms are capable of generating.

FUTURE DIRECTIONS

The problems presented in the foregoing discussion are daunting. If microcosms of various types were not already in operation, a consideration of the problems would be sufficient to convince at least some people that, whatever else microcosms might be good for, they could never be very realistic simulations of such ecosystems as comprise the majority of areas in marine coastal waters.

We cannot overemphasize that no microcosm can ever be an exact replica of nature for several reasons. Because the enclosed system is isolated from the manifold influences to which any similar volume in the natural system is exposed, its behavior will be to some extent modified. Furthermore the natural system is sufficiently variable that it is difficult to select the exact region to be matched, and that region will change rapidly depending on the vagaries of outside influence.

Despite these problems, the evidence from the last few years of experimentation (some of it presented at this symposium) convinces us that microcosms are useful experimental tools. It is evident that many can quite successfully simulate a portion of nature. They behave in a manner sufficiently similar to that of natural reference systems that the differences can be examined thoughtfully to gain insight into the behavior of the natural system. We must keep in mind the stochastic behavior of both natural systems and microcosms and treat this feature as one of the characteristics of both systems.

We have the impression that the chemical behavior of microcosms may be less variable than are most aspects of their biological behavior. Therefore properly designed microcosms may be very useful for biogeochemical studies. If sufficient ancillary information is available to indicate the extent of differences and similarities between the microcosm and the natural reference system, data on the fates and effects of substances in microcosms can be expected to provide realistic guides to fates and effects in natural ecosystems.

We anticipate an increasing use of microcosms designed to simulate real ecosystems. Experimentation with scaling of various parameters will provide additional insight into their effects in nature. Observations on the biological interactions in microcosms have a number of advantages compared with field observations. Migration in or out of the test area can be strictly controlled, so that it is possible to budget the total numbers of individuals of each species present. In addition, relative numbers of a species or an ecological group can be manipulated under conditions that would be difficult or impossible in the field.

The abilities to budget substances and to track many of their routes, pathways, and ultimate fates are most attractive to the biogeochemist. He can make relatively realistic observations in ways impossible in the field and less rewarding in simpler systems. As Strickland (1967) suggested, these complex living models are situated "Between Beakers and Bays" and possess advantages not found at either end of the spectrum.

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